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A NEW *SPIRANTHES* (ORCHIDACEAE) FROM THE CIENEGAS OF SOUTHERNMOST ARIZONA¹

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ABSTRACT

Spiranthes from isolated wetlands in Santa Cruz and adjacent Cochise Counties, Arizona, which in the past have been cited as *S. graminea* Lindl., differ from that species in several floral and vegetative characters and in chromosome number; they are readily separated from it by their few-septate trichomes. The more northern *S. diluvialis* Sheviak is larger-flowered with more ringent flowers and different flower and sepal orientation. The morphological and cytological features of the Arizona plants indicate that they represent a distinct species, described here as *S. delitescens* Sheviak. The cytology of this species suggests an origin through hybridization and amphiploidy, but the parental species are not identified.

Key Words: *Spiranthes delitescens*, *Spiranthes graminea*, *Spiranthes diluvialis*, Cienegas, Arizona

INTRODUCTION

Scattered in the desert grassland of southernmost Arizona are isolated, usually spring-fed wetlands known as cienegas. At one such site northwest of Canelo, Santa Cruz County, P. S. Martin in 1968 discovered a population of *Spiranthes*. These orchids were subsequently determined by Luer as *S. graminea* Lindl. and were the basis for his inclusion of this otherwise Mexican species in the orchid flora of the United States (Luer, 1975). Subsequently, populations of comparable plants have been found at two other sites in Santa Cruz County and one in adjacent Cochise County.

While working on the identity of *Spiranthes diluvialis* Sheviak (Sheviak, 1984), I examined specimens and photographs of the Arizona plants referred to *S. graminea* and found them to differ

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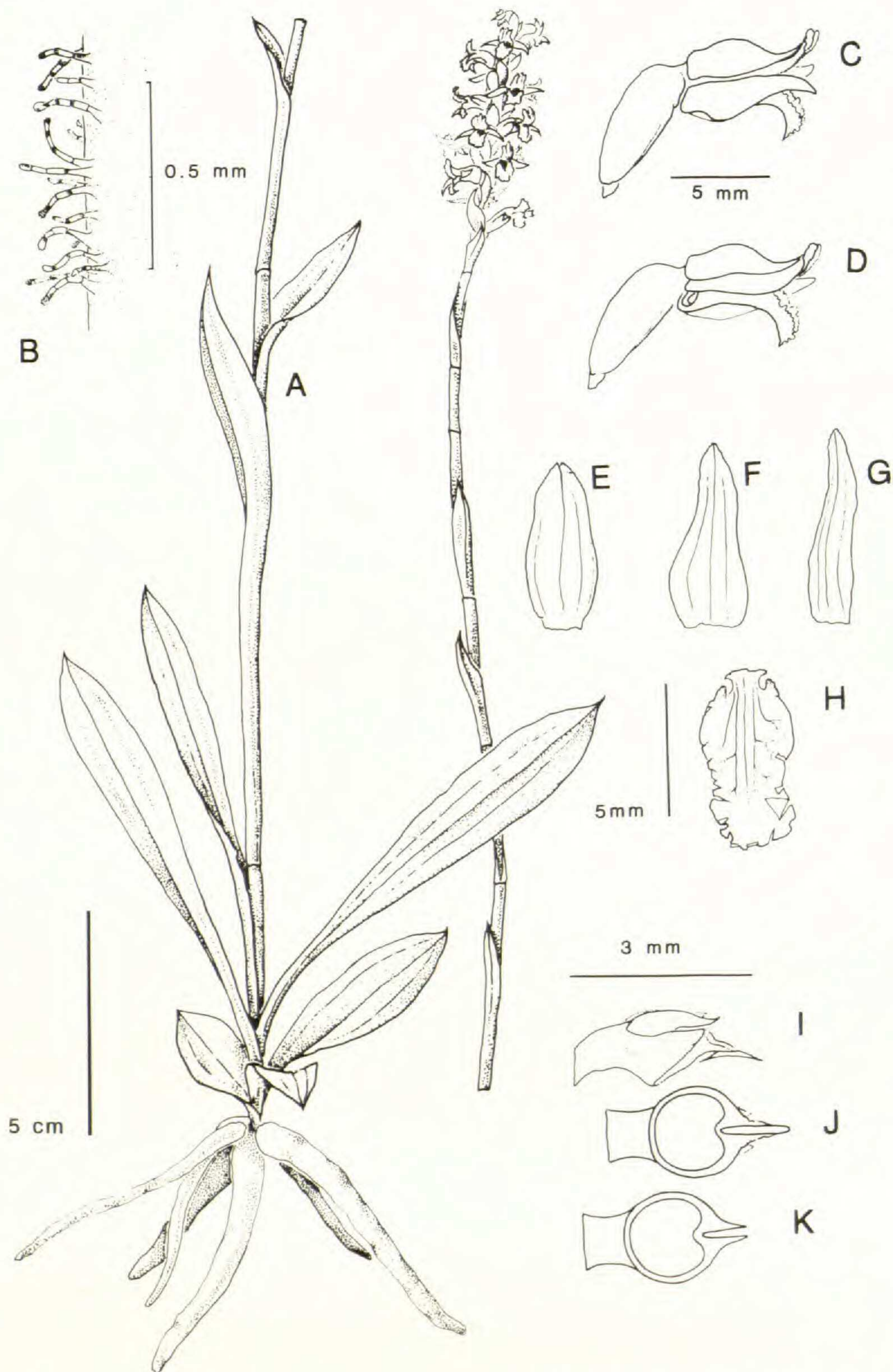


Figure 1. *Spiranthes delitescens* Sheviak. Drawings based on live plants *in hort.* and preserved specimens derived from *Burling s.n.* 'a.' A. Habit. B. Portion of rachis showing trichomes. C–K. Camera lucida drawings from liquid-preserved flowers. C. Flower, lateral view. D. Flower, lateral view, lateral sepal removed.

from Mexican *S. graminea* and to resemble in some features the more northern plants subsequently described as *S. diluvialis*. A live Arizona plant collected for me in 1982 by M. A. Burling (*Burling s.n.*, NYS) bloomed the following year and provided material for morphological and cytological study. Preliminary results indicated that further study was warranted, and in 1984 I studied three of the known populations in the field. Collections from two of these (*Sheviak & Burling 2622, 2626*: NYS), including four live plants, provided additional material for comparison with *S. diluvialis* and *S. graminea*.

An important factor which initially hindered resolution of the problem was our poor state of knowledge concerning *Spiranthes graminea*. From study of specimens and photographs of Mexican plants, it appeared that two entities were included under this name. This situation made comparisons of Arizona and Mexican material difficult. Recently, the problem in Mexico was resolved by Catling and Catling (1988), and their work leading to the recognition of *S. nebulorum* Catling & Catling has provided much of the information necessary to resolve the present problem. Simultaneously, a live plant of *S. graminea* from the State of Mexico (*Kasselmann 56*) was provided by H. W. E. van Bruggen and fixed flowers of *S. nebulorum* (*Greenwood G-885*) were provided by E. W. Greenwood.

Through study of herbarium specimens and of live plants both in the field and under cultivation, the Arizona plants have been found to display a distinct set of morphological and cytological characteristics that clearly distinguishes them from their relatives. Hence, they represent a distinct species:

***Spiranthes delitescens* Sheviak, *sp. nov.* (Figure 1)**

Herba erecta gracilis, persaepe 240–475 mm alta, inferne glabra, superne pubescens. Trichomata 2–5 septata, plerumque apicem versus angustata, capitata pro parte maxima capitulis diametro stipites aequantibus, ecapitata saepe acicularia. Radices tuberoso-incrassatae. Folia lineari-lanceolata vel oblanceolata, radicalia et in caule gradatim bracteis sursum reposita, sub anthesi persis-

←

E. Dorsal sepal. F. Lateral sepal. G. Petal. H. Lip. I. Column, lateral view. J. Column, ventral view. K. Column, ventral view, pollinarium removed.

tentia. Spica persaepe 20–70 mm longa, 13–18 mm diametro. Perianthium 6.5–8.0 (–9.9) mm longum, album. Sepala plerumque ad basim connata, lateralia patenti-arcuascentia necnon plerumque descendencia. Labellum 5.8–7.9 mm longum, oblongum, infra laeve vel obscure verrucosum.

Herb, erect, slender, 240–475 mm tall (rarely shorter), glabrous below, pubescent above. Trichomes 2- to 5-septate, usually tapered toward the apex, of two types, non-capitate ones often acicular, capitate ones with glands mostly about the same diameter as their stipes. Roots tuberously thickened, about 5 mm in diameter. Leaves persisting past anthesis, linear-lanceolate to oblanceolate, the larger to 180 mm long and 15 mm wide (rarely wider), basal and cauline, the latter 5–10 in number and only gradually reduced upward to sheathing bracts 9–17 mm long, the lower half of the stem consequently leafy. Spike rather open to dense, with three flowers per cycle, 20–70 mm long (rarely longer), 13–18 mm in diameter. Floral bracts acuminate to attenuate, the lowermost 8–13 mm long. Flowers tubular, abaxially curved, becoming open with wide-spreading lateral sepals, perianth 6.5–8.0 (–9.9) mm long, white with the center of the lip creamy or very pale yellow. Sepals usually connate basally (the connation below the lip averaging 1.1 mm, up to 2.5 mm but sometimes absent), lanceolate, acute, the lateral curving outward throughout their lengths and usually directed somewhat downward, their apices wide-spreading. Petals for most of their lengths associated with the dorsal sepal, linear to linear-oblanceolate, obtuse, the apices spreading. Lip 5.8–7.9 mm long, oblong, the apex broadly expanded with extensive transverse pleats, smooth to obscurely verrucose below; basal calli stout, .4–1.4 mm long. Column slender; rostellum elongate, deeply bifid.

Chromosome number: $2n = 74$.

TYPE: U.S.A.: Arizona: Santa Cruz Co.: Marshy meadow, seeps, and hummocks in stream, along Turkey Creek, .5 mi. N of Canelo, SE $\frac{1}{4}$ Sec 4, T22S, R18E. elev. 4035 ft. 1 August 1984. *C. J. Sheviak & M. A. Burling 2626* (HOLOTYPE: NYS).

PARATYPES. U.S.A.: Arizona: Cochise Co.: Babocomari Ranch, Babocomari Cienega above the dam. Along old railroad bed in marshy areas. elev. 4600 ft. 25 July 1981. *R. Bailowitz s.n.* (ARIZ); Santa Cruz Co.: O'Donnell Cienega, Knipe Ranch near Canelo, Sec 32 & 33, T21S, R18E. elev. 4950 ft. 7 July 1968. *P. S.*

Martin s.n. (ARIZ); Same locality, 10 July 1968. *P. S. Martin s.n.* (ARIZ); Same locality, 27 August 1969. *P. S. Martin s.n.* (ARIZ); Growing in seep on lower half of slope about 20 ft. south of main spring in bottom of drainage. Sheehy Spring, elev. 4700 ft. Greene (Sharpe) Ranch, San Rafael de la Zanja Grant, San Rafael Valley. 26 July 1980. *L. J. Toolin & F. W. Reichenbacher 936* (ARIZ); Seeping slope, S side of large *Scirpus*-dominated springy meadow. Sheehy Spring, Sharpe [Greene] Ranch, San Rafael de la Zanja Grant, 3 mi. NE of Lochiel, elev. 4700 ft. 1 August 1984. *C. J. Sheviak & M. A. Burling 2622* (NYS); Plants 'a' & 'b' from *C. J. Sheviak & M. A. Burling 2622, in hort.* 1985. *C. J. Sheviak 2750* (NYS); Wet boggy area just N of small pond. Most growing in moist grass with no standing water or on grassy hummocks surrounded by water. Turkey Creek, Canelo Hills. Cienega immediately N of AZ Hwy 83 crossing, Coronado National Forest, SE $\frac{1}{4}$ SE $\frac{1}{4}$ Sec 4 T22S, R18E, elev. 4963 ft. 29 July 1982. *F. Reichenbacher 1374* (ARIZ); Permanently marshy, hummocky meadow along east side of Turkey Creek ca. $\frac{1}{4}$ mi. N of Canelo, Sec 3-4 line, T22S, R18E. 30 July 1982. *M. A. Burling s.n.* (NYS); Same plant as *Burling s.n., in hort.* 1984. *C. J. Sheviak 2667* (NYS); Same plant as *Burling s.n., in hort.* 1985. *C. J. Sheviak 2749* (NYS).

ETYMOLOGY. Present participle of *delitescere*, to hide away, to hide one's self, in allusion to the species' isolated and long-un-suspected occurrence.

Spiranthes delitescens is distinguished by medium-sized flowers of a distinctive shape that is not seen in similar, possibly closely related, species. The flower is characterized by a pronounced ventrally-directed curve such that, in lateral view, the base appears ascending but the apex is horizontal or somewhat nodding. The aspect is of a curved tube. This is in contrast to the ascending flowers of *S. diluvialis* and the horizontal to nodding flowers of *S. graminea* and *S. nebulorum*. Flowers of both *S. diluvialis* and *S. graminea* are relatively slender and ringent; those of *S. delitescens* comparatively short and broad-based; in this respect they are perhaps more like those of *S. nebulorum*. The lateral sepals in *S. delitescens* differ in orientation from these other species: they curve uniformly outward and slightly downward such that the apices approach positions perpendicular to the axis of the flower. In contrast, the basal half of the lateral sepals in the other species are relatively straight: the variably directed sepals of *S. diluvialis* may spread laterally, but they do so from the very base; the apical third may then curve inward or outward. Similarly, in *S. graminea* sepals may be directed outward or outward and upward, but the apices converge above the rest of the flower. In some respects these features of *S. delitescens* are suggestive of *S. porrifolia* Lindl., with its ventrally curved flowers and lateral se-

pals widely outward-curving toward their apices. In other respects, however, *S. porrifolia* is a very different plant with very slender, yellowish flowers with lateral sepals appressed through most of their lengths and lanceolate to lance-ovate, acute lips (see *illustrations* Luer, 1975 and Sheviak, 1989).

The pubescence of *Spiranthes delitescens* is unusual and possibly unique. Glandular-capitate and eglandular trichomes are abundant on the rachis, in common with many species in the genus. In other glandularly pubescent species, however, individual trichomes, whether glandular or eglandular, are of essentially uniform thickness; the glands are notably broader than the stipes, resulting in a distinctly capitate pubescence. In *S. delitescens*, however, trichomes commonly taper toward the apices. Glands are for the most part about the same diameter as their stipes or may be even narrower, and non-glandular trichomes are commonly acicular. In this feature *S. delitescens* suggests *S. vernalis* Engelm. & Gray, which is characterized by acicular trichomes wholly lacking glands.

Many of the other characteristics of *S. delitescens* are those of either *S. graminea* or *S. diluvialis*. Its habit suggests the former: tall and slender with a disproportionately short inflorescence of small flowers, these densely arranged but sometimes disposed in an evident spiral about the rachis. These features are very clearly illustrated in the photographs published by Luer (1975). Leaves are typically much broader than in *S. graminea* and are more typical of *S. diluvialis*, but sometimes even wider than in that species. Roots are tuberous, as in *S. diluvialis*, not slender, wide-spreading, and stoloniferously producing shoots at the apices, as in *S. graminea*. All three species are characterized by pubescent inflorescences. As in most members of the genus, the multicellular, uniseriate trichomes of *S. delitescens* and *S. diluvialis* are composed of but a few cells and hence only 1–5 (usually 2–3, but occasionally –7 in *S. diluvialis*) septate. In contrast, *S. graminea* is remarkable in its very long, 8–11 septate trichomes, a characteristic shared with *S. nebulorum* (Catling and Catling, 1988); this characteristic alone serves to separate clearly *S. delitescens* from these two species. Trichomes of *S. graminea* are furthermore evidently nonglandular (P. M. Catling, pers. comm.) and non-capitate (at least predominantly so), in contrast to the glandularity of the other species. Flowers of *S. delitescens* are markedly smaller than those of *S. diluvialis*, although some overlap occurs, pri-

marily between those of a single known plant of *S. delitescens* with unusually large flowers (*Sheviak & Burling 2622a*) and some depauperate individuals of *S. diluvialis*. Sepals of *S. delitescens* are usually connate at the base to form a short tube (this most evident below the lip); this tube is usually also present in *S. diluvialis*, but in the specimens of *S. graminea* which I have seen, sepals are free to the base. The lip of *S. delitescens* strongly suggests that of *S. graminea*: oblong with a rather minor basal dilation and broad apex sometimes broader than the base, often with extensive transverse pleating of the apical portion. Lip shape in *S. diluvialis* is notably variable, but is characterized by a pronounced basal dilation wider to much wider than the apex. Lip venation is similar in all these species, the nerves relatively few, the laterals with widely diverging branches. The column of *S. delitescens* is slender, suggesting the proportions seen in *S. graminea* and in contrast to the stout columns of *S. diluvialis* and *S. nebulorum*.

CYTOLOGY

Cytology provides a significant background for analysis of the pattern of morphological variation among these species and is important to an assessment of the status of *Spiranthes delitescens*.

Two distinct cytological series of species are known in the genus: a larger group with chromosome numbers based on 15, and a smaller group with numbers based on 22. The latter group includes *Spiranthes romanzoffiana* Cham. and *S. porrifolia*, important species in the West, whereas a few relictual populations of *S. magnicamporum* Sheviak mark the only known occurrence of members of the 15-based series in western North America (Sheviak, 1982, 1984, 1989).

In the present case, numbers were determined or were already known for all species except *Spiranthes nebulorum*, for which cytological material was not available. The single available plant of *S. graminea* (*Kasselmann 56*) yielded a count of $2n = 44$. The unusual situation in the amphiploid *S. diluvialis*, with $2n = 74$ and the formation of 37 bivalents, has already been described (Sheviak, 1984). Six plants of *S. delitescens* from two populations (*Sheviak & Burling 2622a, 2622b, 2622c, 2626a; Burling s.n., s.n. 'a'*) also were all found to be $2n = 74$ with the regular formation of 37 bivalents. Hence, like *S. diluvialis*, *S. delitescens* appears to

be an amphiploid derivative of hybridization between species belonging to the 15- and 22-based series.

MORPHOLOGICAL ANALYSIS

The pattern of similarity in morphological characteristics among the species under consideration here probably reflects in part a shared genetic component of the 22-based cytological series. With the exception of *Spiranthes graminea* and *S. nebulorum*, between which a close relationship is indicated by their unusual pubescence, the morphological similarities in certain features among these species may be due more to group membership than to any specific relationship between species. As a group, the 22-based series exhibits three distinctive features: lips with only a few nerves, the lateral with widely diverging branches; lips varying in shape upon a general pattern of a dilated base and marked subapical constriction; and sepals variably connate at the base to form a short tube. The extreme expression of these conditions is found in the tubular, partially connate calyx and pandurate, typically three-nerved lip of *S. romanzoffiana*; in certain other species one or another of these features may be inconsistently present or wholly lacking.

The cytology of the group, even though incompletely known, imposes certain constraints on the interpretation of morphology and focuses efforts in particular directions. Clearly, despite similarities in habit, flower size, and lip shape, *Spiranthes delitescens* is distinct from *S. graminea*. This distinction is evident from cytology alone, but is supported further by vegetative and floral characters, especially pubescence, floral shape, and lateral sepal position. Although the cytology of *S. nebulorum* is unknown, its evidently close relationship to *S. graminea* and lack of significant characteristics in common with *S. delitescens* remove it from further consideration. In contrast to the other species in the group, the unusual cytology of both *Spiranthes diluvialis* and *S. delitescens* dictates that their relationship must be assessed in considerable detail.

Cultivated Plants

Experience with plants grown indoors under controlled conditions has been useful in delimiting phenotypic variation and in

determining the potential expression of characters. As discussed previously, *Spiranthes* frequently exhibit great phenotypic plasticity. Plants found in a stressed condition in the field may be non-distinctive, often with smaller, rather generalized flowers, but when cultivated under more favorable conditions may produce larger flowers of more distinctive morphology (Sheviak, 1973, 1982, 1989). Even in vigorous plants, the flowers toward the apex of an inflorescence typically are smaller and distinctive features may be poorly expressed (Sheviak, 1982; Catling and Catling, 1988). In the present study, results with live plants addressed problems in interpretation of the evident differences between *S. delitescens* and *S. diluvialis*, and of variability within *S. delitescens* in habit and in shape and size of the flowers.

The habit with very tall, slender, and weak stem topped by a short inflorescence of relatively few flowers that is characteristic of *Spiranthes delitescens* could be a direct product of the plants' habitat. All four of the known stations for the species are dominated by dense sods of tall grasses and sedges. Clearly, the characteristic habit might reflect an etiolated condition. However, under cultivation, both indoors under high-intensity fluorescent light (sufficient to maintain normal habit in other *Spiranthes* grown with *S. delitescens*, including *S. diluvialis*) and outdoors in full sun, the characteristic habit developed.

The density of the inflorescence and the degree to which a single spiral of flowers (the parastichy) is evident varies within individuals. Plants that in the field displayed particularly open inflorescences, in subsequent years under cultivation have produced much denser inflorescences with three evident secondary ranks (orthostichies). Conversely, plants that have, over a period of years, typically produced dense inflorescences, in some cases have in one year developed an evident spiral.

Lateral sepal position and general floral shape vary with the age of the flower; development of the characteristic form illustrated in Figure 1 furthermore requires favorable conditions and may be suppressed in the field. Flowers figured by Luer (1975) are typical of early development; in time, and under appropriate conditions, the sepals spread more widely and the lip, petals, and dorsal sepal spread more fully, producing the broad-faced flower figured here.

Throughout the period of observation of cultivated *Spiranthes delitescens*, a few plants of *S. diluvialis* bloomed sporadically.

When well-grown the *S. diluvialis* were often substantially larger than most plants of that species found in the field, and even when depauperate they did not develop the habit nor the floral characters of *S. delitescens*.

Statistical Analysis

The relatively large flowers of 2622a, plasticity of some floral characters, and especially the paucity of specimens of *Spiranthes delitescens* available for study hampered interpretation. In an effort to determine the significance of perceived differences, a discriminant function analysis (DFA [SPSS PC+: Discriminant]) was performed on 53 specimens: 38 of *S. diluvialis* and 15 of *S. delitescens*. The latter sample includes all known specimens of quality sufficient for inclusion, and actually represents fewer individuals, as 4 of these specimens are cultivated samples of 3 of the field-collected plants included in the analysis. Specimens employed and their geographic origins are cited in Table 1.

Sixteen characters were measured; means, standard deviations, discriminant function character weights, and the order of correlation of characters within the function are presented in Table 2. Most of these characters are self-evident, but a few require clarification. Floral characters were measured in pressed flowers moistened in warm water. Ovary length is the distance from the point of attachment of the median nerve of the lateral sepal to the base of the ovary, which is evident as a dilation above the pedicel (if present). Floral tube maximum basal height measures, in the basal half of the perianth of flowers pressed laterally, the maximum distance from the median nerve of the dorsal sepal to the lower edges of the lateral sepals, the measurement made perpendicular to the axis of the flower. Lateral sepal connation is the length of the connate portion of the lateral sepals below the lip. Sepal separation is the distance separating the adjacent edges of the lateral and dorsal sepals, the measurement made perpendicular to the axis of the flower at its midpoint; positive values result from lateral sepals diverging downward from the dorsal, and negative from laterals rising upward and overlapping the dorsal. Callus length was obtained from the calli lying exclusively on one side of the lip (the right when viewing the inner (upper) surface of the lip with the base uppermost); this technique reduced the

Table 1. Specimens of *Spiranthes diluvialis* and *S. delitescens* employed in the Discriminant Function Analysis.

Locality [County]	Collection	Specimen
<i>S. diluvialis</i>		
Colorado		
Jefferson	<i>Smookley s.n.</i> <i>Sheviak 2224</i> <i>Sheviak 2257</i> <i>Sheviak 2313</i>	COLO NYS 'c' NYS 'holotype,' 'a,' 'b,' '1' NYS '1,' '2,' '3'
Nevada		
Lincoln	<i>Hall s.n.</i>	BRY
Utah		
Garfield	<i>Neese & White 3927</i> <i>Sheviak 2300</i>	BRY 'a,' 'b' NYS 'a,' 'b,' 'c,' 'd,' 'e,' 'f,' '4,' '5,' '6'
Salt Lake	<i>Jones 1908</i> <i>Nielsen 221</i>	MICH 'c'; MSC 'right' UT 'a,' 'b,' 'c,' 'd,' 'e'
Tooella	<i>Cottam 14361</i>	ARIZ 'b'; UT 'a,' 'b,'
Utah	<i>Barnett 154</i>	BRY 'a,' 'b'
Wayne	<i>Neese & White 3904</i>	BRY 'b,' 'c'; DAV 'a'
Weber	<i>Tracy 169/236</i> <i>Tracy & Evans 554</i>	MSC NY 'a'
<i>S. delitescens</i>		
Arizona		
Cochise	<i>Bailowitz s.n.</i>	ARIZ 230519
Santa Cruz	<i>Burling s.n.</i> <i>Martin s.n.</i> <i>Martin s.n.</i> <i>Reichenbacher 1374</i> <i>Sheviak 2667</i> <i>Sheviak 2749</i> <i>Sheviak 2750</i> <i>Sheviak & Burling 2622</i> <i>Sheviak & Burling 2626</i> <i>Toolin & Reichenbacher 936</i>	NYS ARIZ 167218 ARIZ 167219'b' ARIZ NYS NYS NYS 'a,' 'b' NYS 'a,' 'b,' '2' NYS 'a,' '1' ARIZ 'b'

opportunity for bias arising from the often different lengths of the two calli on each lip.

Groups for the analysis were defined geographically: the more northern *Spiranthes diluvialis* from the Great Basin and the base of the Front Range in Colorado, and the plants from southernmost Arizona. Two distinct groups were recognized by DFA (Figure

Table 2. Means, standard deviations, discriminant function character weights, and order of correlation within the function for characters measured in the 53 specimens of *Spiranthes* cited in Table 1. Constant = 5.297525.

Character	Means (σ)		Discriminant Function Character Weights (Correlation)
	<i>S.</i> <i>diluvialis</i>	<i>S.</i> <i>delitescens</i>	
BRACTS/LEAVES			
Cauline: number	6.0 (1.8)	7.3 (1.7)	.2395277 (9)
Cauline: length of uppermost	20.2 (7.2)	12.3 (2.4)	.1868922 (5)
Floral: length of lowermost	16.7 (5.2)	10.5 (1.6)	-.3243319 (4)
INFLORESCENCE			
Length	73.2 (28.7)	52.4 (21.7)	.006118466 (8)
OVARY			
Length	4.1 (1.2)	4.0 (0.8)	.9171546 (15)
Width	3.0 (0.8)	2.7 (0.5)	-.2975654 (12)
FLORAL TUBE			
Maximum basal height	3.4 (0.6)	3.2 (0.5)	.1886418 (11)
SEPAL			
Separation	-0.3 (0.6)	0.3 (0.4)	.3421256 (6)
Dorsal: length	10.0 (1.5)	7.2 (1.2)	.2877804 (3)
Lateral: length	10.5 (1.2)	7.7 (0.8)	-.6379773 (1)
Lateral: connation	0.6 (0.6)	1.1 (0.7)	1.291342 (7)
LIP			
Length	8.9 (1.0)	6.8 (0.6)	-.7362284 (2)
Maximum basal width	4.4 (0.9)	3.9 (0.5)	-.7828668 (10)
Minimum median width	2.4 (0.7)	2.4 (0.4)	.6284711 (16)
Maximum apical width	3.2 (0.8)	3.3 (0.6)	.1752346 (14)
Callus length	0.8 (0.3)	0.9 (0.2)	.8802953 (13)

2), and these corresponded to the groups established geographically. No specimens were misclassified (assigned by geographic origin to one group but morphologically referable to the other).

DISCUSSION

Status of *Spiranthes delitescens*

The cytology of *Spiranthes delitescens* indicates an amphiploid origin involving hybridization of species from each of the two cytological series of the genus, those based on 15 and 22 chro-

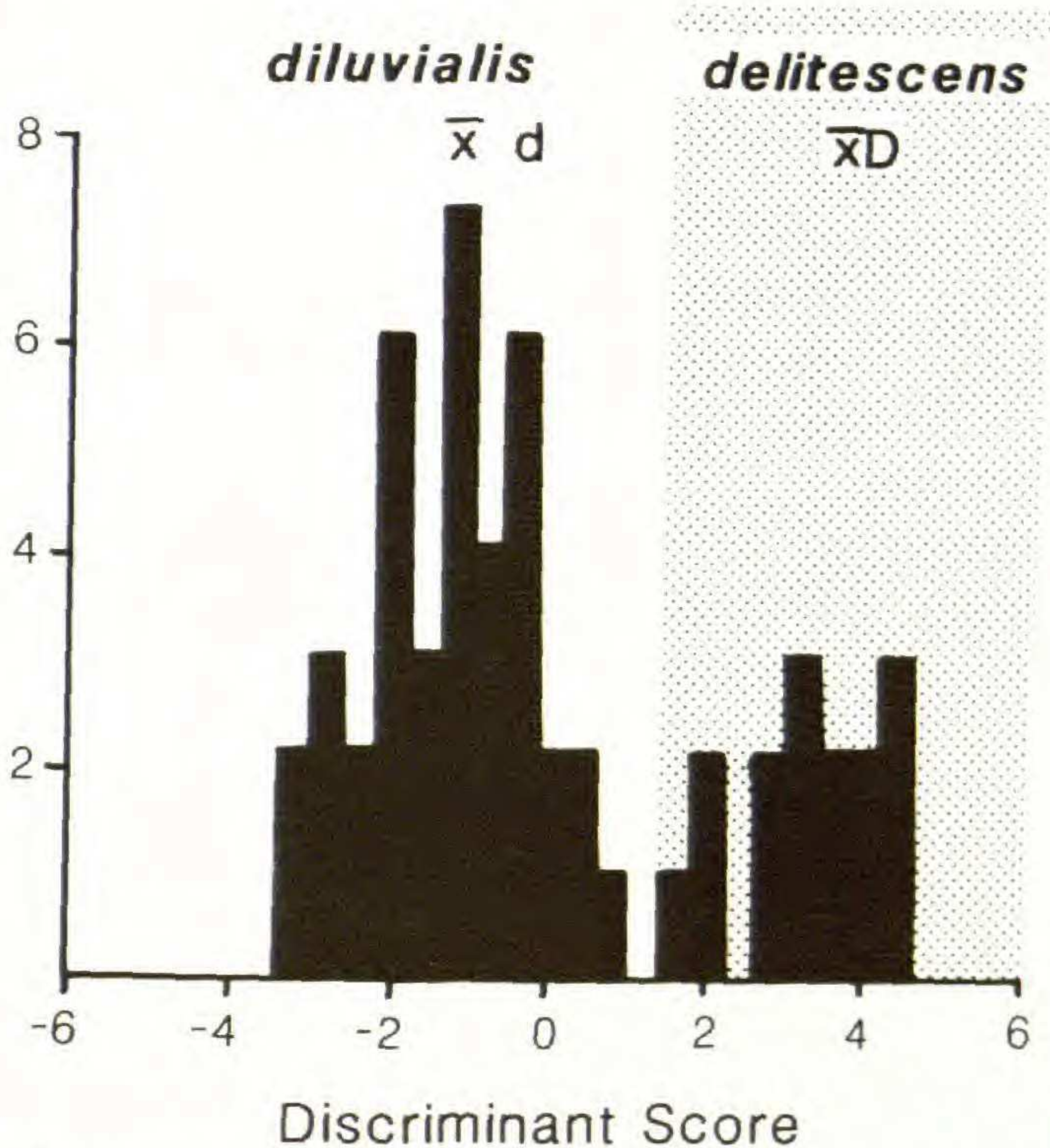


Figure 2. Discriminant scores of 38 specimens of *Spiranthes diluvialis* and 15 of *S. delitescens*. Also plotted are group centroids (\bar{x}) and the holotypes of *S. diluvialis* (d) and *S. delitescens* (D).

mosomes. Such an origin is shared with *S. diluvialis*. The status of *S. delitescens* consequently depends on its relationship with this species. Do the two taxa have a common origin, are they the results of separate crosses between the same species, do they share a single parent, or are their similarities due to relationships between their parents? The morphological data are sufficient to demonstrate that *S. delitescens* arose independently from *S. diluvialis*, but an understanding of its origin is elusive.

The results of DFA indicate that, indeed, *Spiranthes delitescens* is morphologically distinct from the more northern *S. diluvialis*, but these results are not necessarily inconsistent with an hypothesis of long isolation and drift of a limited gene pool. Perhaps *S. delitescens* merely represents the small end of a discontinuous range in size of various characters within *S. diluvialis*. Most of the characters summarized in Table 2, including the five most strongly discriminating, show *S. diluvialis* to be the larger. Connation of the lateral sepals, however, is markedly greater in *S. delitescens*, despite the overall smaller flower size, and callus length also averages slightly greater in this species. The number

of cauline bracts and leaves is usually greater in *S. delitescens* than in the somewhat shorter *S. diluvialis*; this difference probably is not the result of a simple relationship between bract number and stem length, because a broader study of the *S. romanzoffiana* complex suggests that bract number may differ between taxa regardless of the stature or vigor of individuals or the conditions under which they may be growing.

The orientation of the lateral sepals of *Spiranthes delitescens* is unlike that of any otherwise similar species. This feature involves both the curving of the sepals and their position relative to the dorsal sepal. Similarly, the curve of the flower of *S. delitescens* as viewed from the side is not seen in *S. diluvialis*. The unusual pubescence of *S. delitescens* is particularly significant, because infraspecific variation sufficient to accommodate such trichomes within *S. diluvialis* is simply unknown in the genus. These unique features of *S. delitescens* are furthermore not those of either of the apparent parents of *S. diluvialis*, i.e., *S. romanzoffiana* and *S. magnicamporum*. Hence the origin of *S. delitescens* seems quite clearly to have been through hybridization of different species than was that of *S. diluvialis*, dictating that these two taxa be treated as distinct at the specific level.

Spiranthes delitescens is the third species of the genus to be described from the western United States in recent years. Along with a few disjunct occurrences of *S. magnicamporum* now known in the region and Catling and Catling's recent work in Central America, no available key adequately treats the genus in this geographic area. Accordingly, a key to the species in western North America and in Central America is included here. For Central American species it is based, largely verbatim, on the key of Catling and Catling (1988).

KEY TO *SPIRANTHES* IN WESTERN NORTH AMERICA AND
CENTRAL AMERICA

1. Rachis and upper portion of stem densely pubescent; the longest trichomes .4–.6 mm long, 8–11 septate; flowers relatively small, perianth 5–7 mm long. (Central America) . . . 2
2. Lip oblong-ovate or oblong-quadrate, not strongly curving from the claw and the floral tube straight and not widened basally; basal calli .4–.8 mm long; lateral sepals 1.2–1.8 mm wide *S. graminea* Lindl.

2. Lip broadly ovate, strongly curving upward from the claw and consequently the floral tube arched and widened basally; basal calli .9–1.8 mm long; lateral sepals 1.7–2.8 mm wide *S. nebulorum* Catling & Catling
1. Rachis and upper portion of stem glabrous to densely pubescent, the trichomes 1–5 (rarely to 7) septate; flowers various, perianth 4–14 mm long 3
3. Rachis and upper portion of stem densely pubescent, trichomes all non-capitate and tapering to often sharp-pointed apices; flowers in an evident, open spiral
. *S. vernalis* Engelm. & Gray
3. Rachis and upper portion of stem glabrous to rather densely pubescent, many of the trichomes glandular-capitate; flowers in an open to very tight spiral, the inflorescence then dense and the primary coil of flowers obscure . . . 4
4. Glands of the capitate trichomes inconspicuous, mostly about the same diameter as the stipe or smaller; trichomes commonly tapered toward the apex, the non-capitate often acicular; lip oblong; lateral sepals arcuate spreading. (Southern Arizona)
. *S. delitescens* Sheviak
4. Glands of capitate trichomes conspicuous, markedly broader than the stipe; trichomes of uniform thickness below the gland, the non-capitate blunt or truncate; flowers various 5
5. Flowers in a very open spiral with many more than 5 flowers per cycle 6
6. Lip ovate or elliptical, center of lip green. (Central America) . . . *S. tortile* (Thurn.) Garay & Sweet
6. Lip pandurate, white. (California & Oregon) . . .
. *S. romanzoffiana* Cham.
(a local race, possibly a distinct taxon)
5. Flowers in an open to very tight spiral, 3 or 4 secondary ranks then evident, usually 3 and not more than 5 flowers per cycle 7
7. Rachis glabrous or sparsely pubescent, the longest trichomes less than .18 mm long (usually much less), the glands often sessile or subsessile; sepals connate at the base 8
8. Lip broadest at the base, membranaceous,

- white or ochroleucous; perianth 8–12 mm long (rarely shorter) 9
9. Lip pandurate, the apex dilated, glabrous above; sepals & petals united throughout their lengths and forming a hood
 *S. romanzoffiana* Cham.
9. Lip ovate to lanceolate, the apex only slightly or not at all dilated, with a dense cushion of peg-shaped trichomes above; sepals & petals with apices free & spreading *S. porrifolia* Lindl.
8. Lip broadest near the middle; the base distinctly narrowed, thick and fleshy, green; perianth 4–6 mm long
 *S. infernalis* Sheviak
7. Rachis sparsely to densely pubescent, the longest trichomes .19 mm long or longer (often much longer; very rarely shorter, then the lip not pandurate and the sepals and petals not united nor forming a hood), the glands obviously stalked; sepals fused at the base or free 10
10. Lip without a marked subapical constriction, calli short, conical; sepals free to the base; flowers nodding; leaves wholly basal, fugaceous, usually absent at anthesis
 *S. magnicamporum* Sheviak
10. Lip with a marked subapical constriction, the base usually dilated, calli often elongated; sepals often basally connate; flowers ascending; a few leaves on the base of the stem, persisting through anthesis
 *S. diluvialis* Sheviak

Origin of *Spiranthes delitescens*

The distinctive features of *Spiranthes delitescens* include habit, pubescence, floral shape, sepal orientation and connation, and lip shape and venation. These should serve to indicate at least one of its parents, but the origin of the characteristics is unknown. Lip venation in *S. delitescens* is typical of the condition seen in all members of the 22-based series; lip shape, with minor sub-

apical constriction, may represent merely a suppression of this feature by the parent from the 15-based series. The general habit of *S. delitescens* suggests that of *S. graminea*, and the lips of these species are very similar. The free lateral sepals which I have seen in specimens of *S. graminea*, however, if typical, would seem to preclude the species as a parent, because of the marked sepal connation in *S. delitescens*: this feature must come from the 22-based parent. Floral shape and sepal orientation suggest *S. porrifolia*, with its narrowly curving flowers and lateral sepals curving outward toward the apices; this member of the 22-based series would seem to be a possible contributor of these features. The other parent in such a cross is not obvious. Indeed, of known extant western species, *S. graminea* and *S. porrifolia* would seem to provide the proper combination of salient features, but such a cross is not in keeping with the cytological evidence.

The pubescence of *S. delitescens* suggests ancestry involving *S. vernalis*. Significantly, an artificial hybrid of *S. vernalis* and *S. odorata* (Nutt.) Lindl. (Sheviak 2569) is densely pubescent with tapering trichomes, the capitate ones with reduced glands. The habit of this plant furthermore is very similar to that of *S. delitescens*, with long slender stem bearing leaves at the base and short, rather dense inflorescence with flowers smaller than those of either parent. Hence *S. vernalis* could indeed serve as a parent: the shape of its trichomes is conveyed, even affecting the size of the glands, which are thus suppressed but nonetheless present; the open spiral of its inflorescence is missing, and a habit suggesting that of *S. delitescens* is produced, even with the large, stout *S. odorata* as the other parent. The curved flowers of *S. delitescens* are not predictable products of a cross of *S. graminea* and *S. vernalis*, however. The tuberous roots of *S. delitescens* are likewise not to be expected, but this feature is not so pronounced as in some other species, and they are perhaps not unlike roots in some *S. vernalis*.

That an artificial hybrid employing *Spiranthes vernalis* and *S. odorata*, a plant without any particular similarity to *S. delitescens*, could in fact simulate this species in habit and pubescence suggests that *S. vernalis* might indeed be a parent, and that a cross with the tuberous-rooted *S. porrifolia* is a possibility. Such a cross might yield the appropriate floral shape and would be expected to produce suitably curved lateral sepals. Arguing against such an origin is the present wide separation of the ranges of these two

species. Although *S. vernalis* is widespread in the southern plains and may have occurred in the Southwest during the Pleistocene, as was apparently the case with *S. magnicamporum* (Sheviak, 1984), the current disjunct populations which support such an interpretation for the latter species are not known for *S. vernalis*.

Although the morphological evidence allows some speculation, the largely unknown genetics of the group, as emphasized by some of the characteristics of the artificial hybrid mentioned above, emphasizes the difficulty in identifying ancestral species. The origin of *S. delitescens* is thus obscure.

A NOTE ON RARITY

I visited all of the four known stations for *Spiranthes delitescens* and located the plant at three (time at the fourth was inadequate to assess the status of the plant, but the habitat, at least, was intact). Martin's original discovery site was acquired by The Nature Conservancy and is managed as one of their preserves. The status of the species on the preserve is a prime focus of attention. The species is abundant at Sheehy Spring, but is very restricted within a larger area of seemingly suitable habitat. The population along Turkey Creek is the most extensive and may cover a greater area than the specimen data indicate. Although one expects the species to be found at additional sites in the future, the nature of its habitat severely limits the possibilities. It is almost certain that *S. delitescens* occurs in Mexico, perhaps widely so, but P. M. Catling reported (pers. comm.) that he had not encountered specimens during his work. Whatever its distribution in Mexico may prove to be, it is clear that *S. delitescens* is extremely rare and restricted in the United States.

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